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The population dynamics of Daphnia pulex Leydig 1860 and Daphnia schodleri Sars 1862 under temporary pond conditions.

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THE POPULATION DYNAMICS OF DAPHNIA PULEX LEYDIG 1860 AND DAPHNIA SCHØDLERI SARS 1862 UNDER TEMPORARY POND CONDITIONS

by
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ABSTRACT

A study of a temporary pond located on the grounds of the sanitary landfill area of the city of Windsor, Ontario, was conducted from March 4, 1970, when the pond thawed, to July 24, 1970 when the last sample was taken before the pond completely dried up. The object of this study was to attempt to determine if the temporary nature of this habitat had modified the life cycles of *Daphnia pulex* and *D. schødleri*, the two *Daphnia* species present in the pond.

A twice weekly sampling programme determined physical, chemical and biological characteristics of the pond. Nitrogen, phosphate, chlorophyll *a*, oxygen, and turbidity were the highest prior to the pond drying. Total alkalinity decreased sharply at this time.

Zooplankton consisted of three cladoceran species: *D. pulex*, *D. schødleri*, and *Moina rectirostris*; and two copepod species: *Diaptomous leptopus* and *Cyclops bicuspidatus thomasi*.

To examine the influence of the temporary pond on the life cycles of the *Daphnia*, age of reproductive maturity, clutch size, and ephippial production were examined. The influence was most apparent on *D. pulex* which probably reached reproductive maturity by the fourth instar. Clutch size was not enhanced, but the rate of ephippial production was high throughout most of the life cycle. *Daphnia schødleri* did not mature at an earlier instar, nor was its clutch size

larger. However, ephippia were produced in substantial numbers throughout its life cycle. It is suggested that the selective pressures of the temporary pond on *D. pulex* are probably greater than the selective pressures on *D. schødleri*.

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INTRODUCTION

Animal populations are regulated by intrinsic and extrinsic factors working together to produce a combined effect. In *Daphnia*, such intrinsic factors as age, size and clonal characteristics have been correlated with egg number and size, and egg development (Green 1956). The most important extrinsic factors are those of food, temperature, oxygen concentration, and population density (Green 1966). These factors, interacting with environmental parameters effect the density of the population, the number and size of the young, and the population dynamics of this genus.

A number of workers have studied these aspects of population control in the Cladocera: MacArthur and Baillie (1929), Pratt (1943), Slobodkin (1954), Green (1956), Smith (1963), Hall (1964), and others. Hazelwood (1964) has reviewed the literature for *Daphnia*.

MacArthur and Baillie (1929) have shown correlations between sex, temperature, and longevity in *Daphnia magna*. Longevity was an inverse function of temperature, with males being most sensitive to temperature extremes. Hall (1964) concluded that food and temperature had separate effects on *Daphnia galeata*. Temperature principally influenced the frequency of molting and reproduction, duration of egg developement and longevity; food principally influenced the growth per instar.

Many authors have studied the effects of density on different populations of *Daphnia*. Pratt (1943) postulated a direct density effect as a limiting factor in laboratory populations of *Daphnia magna*. At 25°C the birth rate was an inverse function of the population density, whereas at 18°C the effect of density was similar but less severe. However, Slobodkin (1954) believes that it was highly unlikely that a direct density effect exists for *Daphnia* populations. His argument was based on a linear relationship between population biomass and food supply. The minimum range of population density legislated solely by available food was 1-10 animals per cc of medium. This was higher than any recorded density in nature. Although crowding is a difficult factor to separate from food shortage, Warren (1900) and Langhans (1909) reported a diminution in egg production caused by crowding, even in the presence of abundant food. Frank *et.al*. (1957) reported that increased density decreased birth rate, lowered growth rate, and increased survival.

In *Daphnia*, several factors have been reported that influence egg production. Low oxygen content of the water can have an effect on egg production. If the oxygen drops below 2 or 3 ppm, the number of eggs produced by *Daphnia obtusa* decreases in proportion to any further decrease in oxygen concentration (Fox, Gilchrist and Phear, 1951). Egg size and clutch size are influenced by food and temperature (Green, 1966). Lower temperatures favor the production of larger eggs, and a larger clutch size. At lower temperatures *Daphnia* develop slower but grow to a larger size.

Green (1956) showed that an increase in size was directly correlated to an increase in egg number and size. Green (1966) noted that lake dwelling species of Daphnia produced fewer but larger eggs than the pond dwelling species of the same size. Daphnia pulex produced much larger eggs in Lake Ohrid, Yugoslavia, than it did in British ponds (Green,1964). Green suggests a correlation between larger eggs in lakes and lower availability of food. He states that a larger egg will have a better chance of survival by reaching maturity after fewer instars. In warm water with ample food supply, the larger clutch size of smaller eggs ensure a greater population growth rate.

Daphnia have two methods of reproduction: parthenogenesis and sexual. In what has often been called "favorable" environmental conditions, Daphnia reproduce parthenogenetically. In "unfavorable" conditons, males appear among the offspring to fertilize sexual eggs. The fertilized egg is termed an ephippium that can withstand both freezing and dessication. Due to a high rate of parthenogenetic reproduction, genetically homozygous populations are easily obtained. For this reason most authors tend to ignore genetic factors as relevant in Daphnia population studies. Slobodkin(1954) was careful to point out that although males are usually in very low numbers, they do exist and thus permit some genetic exchange. Mutation and crossing over are also possible.

The pond studied was selected because of its temporary nature and its abundant Daphnia populations. The object of this study was to attempt to determine if the temporary nature of this habitat has a modifying effect on the life cycle of the Daphnia populations.

DESCRIPTION OF THE POND

The populations of Cladocera discussed in this thesis were located in a temporary pond on the grounds of the sanitary landfill area of the city of Windsor, Essex County, Ontario, 200 meters west of Malden road (83° 3' 36" west and 42° 16' 30" north) and 2.6 miles from the University of Windsor. The pond elevation is 179.8 m above sea level.

The pond area is part of a smooth clay plain that overlies limestone bedrock (Oud 1970). Interspersed with sandy bars, the area is classified as a mixture of Plainfield and Berrien sand (Richards *et al*, 1949).

Although the pond is located in the sanitary landfill, the dumping area is west of the pond so no garbage is found around or in the pond. Air pollution from the cities of Detroit and Windsor probably contribute substantially to the mineral concentration, but the extent is unknown.

The pond has no inlet or outlet and the water levels are determined largely by ground seepage, surface runoff, and evaporation. The Fall and Spring rains, as well as the melting of accumulated snow and ice are probably the most important factors in re-establishing the pond's existance from year to year. As a result of the summer's lower precipitation and warmer temperatures, evaporation is usually sufficient to dry out the pond.

The morphometric measurements are recorded in Table I.

The dominant vegetation was represented by the emergent

TABLE I

MORPHOMETRY OF TEMPORARY POND

PARAMETER	MEASUREMENT
Maximum depth	0.65 m
Maximum length	40.2 m
Maximum breadth	12.9 m
Mean breadth	12.2 m
Mean depth ($\bar{d}$)	0.55 m
Area (A)	0.0478 hectares
Volume ($V=\bar{d}A$)	265.5 m^3

POND MAP

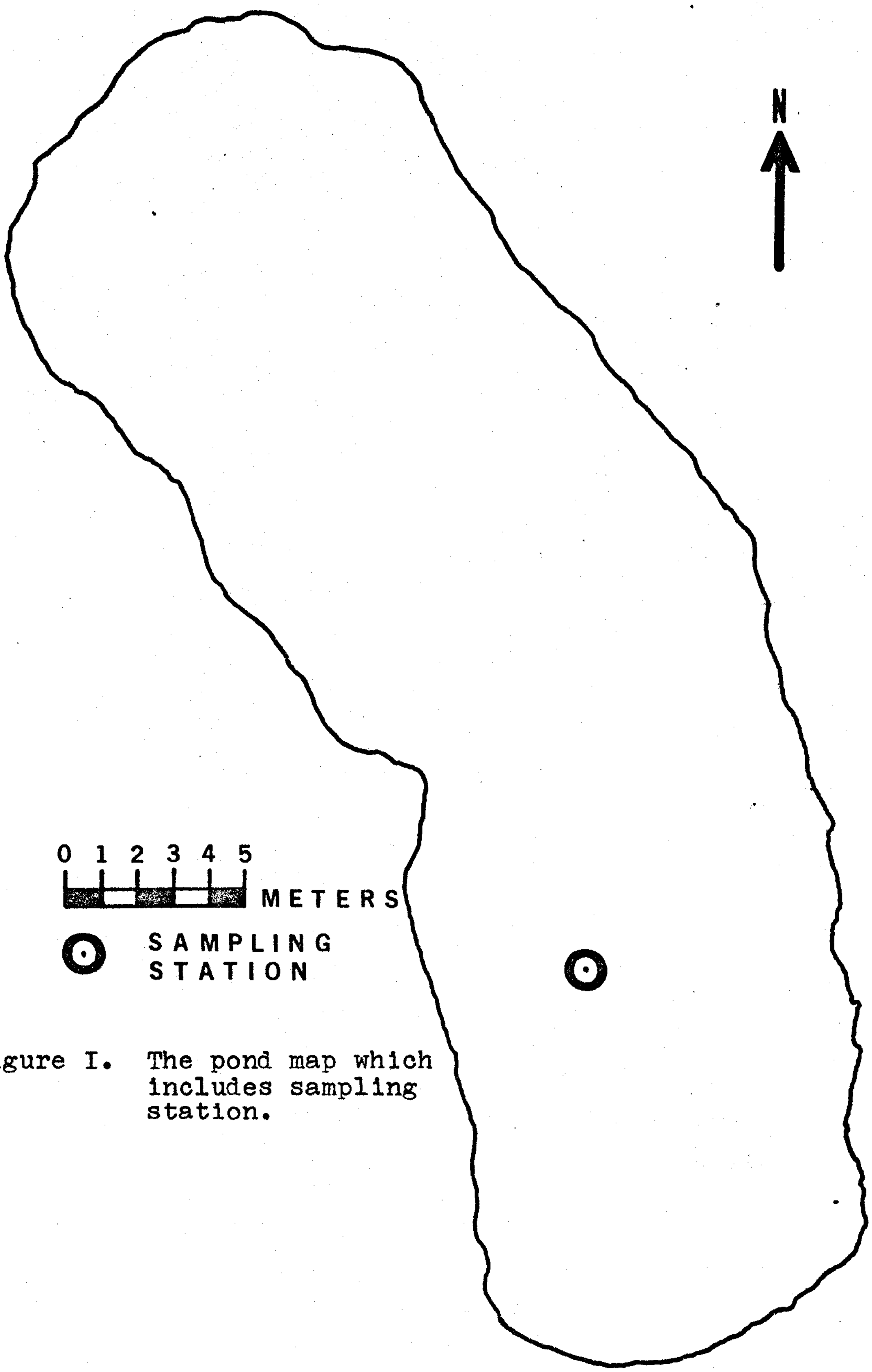


Figure I. The pond map which includes sampling station.

species Typha angustifolia L. and some Typha latifolia L. Also present were Alisma sp. and Juncus sp. No floating species were present.

Invertebrates found in the pond were coleopteran Dinuetes sp., the hemipterans Notonecta sp. and Gerris sp. Occasionally aquatic mites, the fisher spider Dolomedes triton, as well as the dipteran Chaobourus sp. were found in the plankton samples.

Vertebrates found in or around the pond were the painted turtle Chrysemys picta, Rana pipians and a Bufa sp. Northern Fathead minnow young-of-the-year, Pimephales promelas promelas, were found in some plankton samples, but never in large numbers.

METHODS AND MATERIALS

A twice weekly sampling programme was established to determine physical, chemical, and biological characteristics of the pond. The sampling period was from March 4, 1970, when the pond thawed, to July 24, 1970 when the last sample was taken before the pond had completely dried. All samples were taken at 10:30 am.

Air and surface water temperatures were measured in degrees centigrade using a glass mercury filled thermometer. Dissolved oxygen, carbon dioxide, and pH were determined at the pond using the Hach Chemical test kit. For these tests water was collected using a PVC plastic tube water sampling bottle.

Water samples were analyzed upon return to the laboratory. Alkalinity and hardness were determined using the Hach Chemical Company portable water engineers laboratory. Total notrogen, phosphate, and turbidity were determined using the Hach Chemical Company water and waste water analysis colorimetric procedures as adopted for the Bausch and Lomb Spectronic 20 Colorimeter.

A uniform series of 10 liter quantitative plankton samples was collected from 5 to 10 cm below the surface (if the water was sufficiently deep) by means of a two liter calibrated pitcher, and concentrated to a volume of 97 cc by means of a Wisconsin net of 28 micron aperture nylon mesh. Plankton adhering to the side of the net was washed into the sample by means of a wash bottle spray of distilled water. Three cc of 40 per cent neutral formalin (pH-7.4) were then added to the samples. A qualitative sample was also taken to aid in identification.

Plankton samples were examined in the laboratory with the aid of Olympus and Wild binocular microscopes. The plankton population density was enumerated by means of a 1 cc Sedgewick-Rafter counting cell according to techniques outlined in Welch (1948). Identification was based on Ward and Wipple (1959) and Brooks (1957).

One liter samples were also collected for pigment extraction at the same time that the plankton and water samples were collected. Techniques for pigment extraction were performed largely according to those described by Richards and Thompson (1952). The equation for chlorophyll a was obtained from SCOR/UNESCO Working group on photosynthetic pigments (SCOR/UNESCO 1966).

In order to measure daphnid length, a Reichert Visopan microscope was calibrated with an American Optical Micrometer. The daphnids were measured from the crown of the head to the base of the tail spine using the techniques of Green (1954). Egg numbers per brood pouch as well as egg type (parthenogenetic or ephippial) were counted to determine the clutch size and the degree of ephippial production.

Normally the maturity of daphnids is easily established: if eggs are present in the brood chamber, the daphnid is mature. But Hall (1964) has reported that preservation in formalin often causes eggs to be released from the brood pouch. Since the total number of mature daphnids was needed to determine the degree of ephippial production, it was necessary to establish a minimum adult length for which an eggless daphnid could be considered adult. The immature eggless instar could therefore be distinguished from the mature "eggless" instar.

In this study, females are considered mature if their body length is greater than two standard deviations below the mean body length for that species. Since growth between molts is relatively large in the early instars (Anderson *et al*, 1937), the distinction between immature instars and mature instars is not a fine one, and based on size, it is unlikely that immature daphnids would be included as adults. This is further discussed below (p. 24-26).

The two species of *Daphnia* examined were *D. pulex* and *D. schødleri*.

RESULTS

A. Physical Results

Physical factors are summarized in Table II. Graphs for these factors appear in Figure 2.

The water temperature closely followed the air temperature and ranged from 0° C when water first began to appear under the ice, to a high in summer of 28° C. The pond was completely frozen to the bottom during the winter with open water appearing by March 20, 1970.

The turbidity ranged from a high in summer of 665 Jackson Units (J.U.) to a low in April of 37 J.U., and averaged 152 J.U. for the duration of the study. In general, increases in turbidity were related to rainfall and the drying up of the pond. During the last two weeks that water was present in the pond the turbidity averaged 540 J.U.. The lowest turbidities were recorded during the thaw and while the pond was still relatively deep.

B. Chemical Results

Chemical factors are summarized in Table III. Graphs for these factors appear in figures 3 and 4.

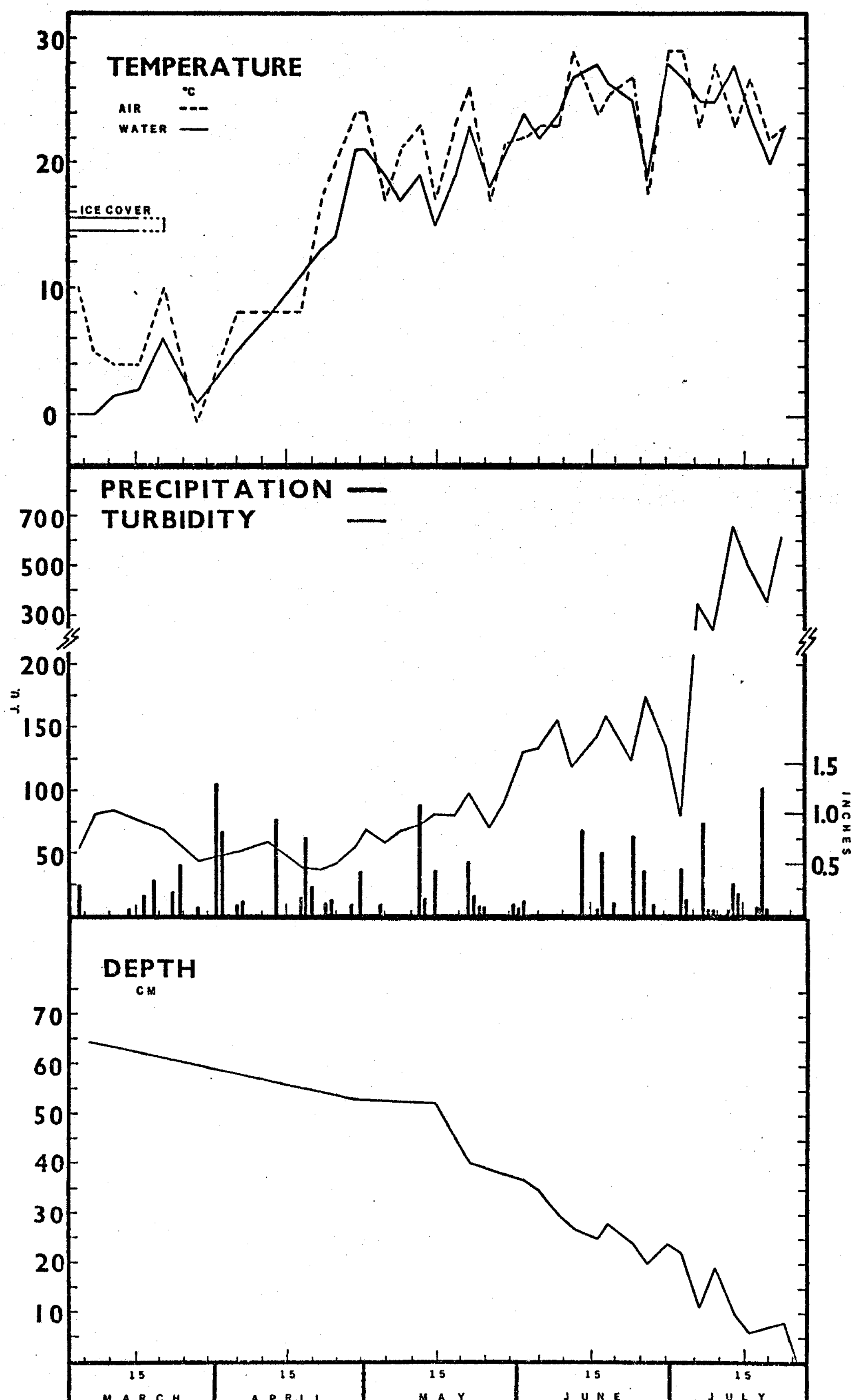
The pH (Fig.3) remained alkaline throughout the study period ranging from 8.0 to 9.6. The study average was 8.8. Generally the pH was fairly constant, but rising to pH 9.6 just prior to the pond drying out.

The dissolved oxygen concentrations (Fig. 3) ranged from 3.2 ppm to 16 ppm, averaging 8.4 ppm. Generally, the

TABLE II. SUMMARY OF PHYSICAL FACTORS

		March	April	May	June	July	Study Average
Depth (cm)	High	65	53	52	37	22	
	Low	-	-	40	20	0	28.2
	Mean	-	-	46	26.7	12.7	
Temperature Air (°C)	High	10.0	24.0	26.0	29.0	29.0	
	Low	-0.5	8.0	15.0	17.5	22.0	18.6
	Mean	3.7	14.1	20.8	23.3	25.0	
Temperature Water (°C)	High	6.0	21.0	23.0	19.0	28.0	
	Low	0.0	5.0	15.0	28.0	20.0	17.5
	Mean	1.7	11.9	19.1	24.8	24.6	
Turbidity (J.U.)	High	84	59	99	175	665	
	Low	44	37	59	125	81	152
	Mean	66	47	77	143	406	

Figure 2. Air and water temperatures, turbidity, precipitation and depth of the pond from March 4, 1970 to July 24, 1970.


TEMPERATURE
°C
AIR
WATER
ICE COVER
30
20
10
0
PRECIPITATION
TURBIDITY
700
500
300
200
150
100
50
J.U.
1.5
1.0
0.5
INCHES
DEPTH
CM
70
60
50
40
30
20
10
15
MARCH
15
APRIL
15
MAY
15
JUNE
15
JULY

oxygen concentrations fluctuated the most once the water had warmed (by the beginning of May). During the last two weeks in which water was present in the pond, the dissolved oxygen concentration rose from 5 ppm to 16 ppm. This dramatic increase in oxygen concentration was related to an Euglenoid bloom that is reflected in the chlorophyll a concentrations (Fig. 4).

Total alkalinity (Fig.3) ranged from 20 ppm to 240 ppm with a study average of 148 ppm. With only two exceptions (May 21 and May 28), the total alkalinity was due to Bicarbonate. Prior to the drying out of the pond, the total alkalinity decreased sharply. The lowest value of the entire study was recorded at this time (20 ppm).

Total hardness (Fig. 3) ranged from 85 ppm to 454 ppm, with a study average of 211 ppm. Total hardness was due to both Calcium and Magnesium ions. Contrary to alkalinity, the total hardness increased just prior to the pond drying out.

Total nitrogen (Fig. 4) ranged from 0.4 ppm to 4.41 ppm, with a study average of 0.86 ppm. Generally the total nitrogen concentrations were continually fluctuating with 1.21 ppm at the beginning of the study, then dropping to a low of 0.4 ppm (May 1). A peak of 4.41 ppm occured on May 22. Similar to total hardness, the total nitrogen concentrations were also very high prior to the pond drying out.

Total phosphate (Fig.4) ranged from 0.02 ppm to 0.53 ppm. The study average was 0.18 ppm which was well above

TABLE III. SUMMARY OF CHEMICAL FACTORS*

		March	April	May	June	July	Study Average
Iron	High	0.77	0.65	0.94	2.07	7.80	
	Low	0.33	0.33	0.52	0.60	1.15	1.52
	Mean	0.59	0.44	0.72	1.48	4.20	
Oxygen	High	13.0	12.0	11.0	9.0	16.0	
	Low	9.5	5.0	4.0	3.2	5.0	8.4
	Mean	11.6	9.6	7.0	5.7	10.0	
pH	High	9.5	9.0	9.0	8.8	9.6	
	Low	8.0	8.0	8.7	8.0	8.6	8.8
	Mean	8.6	8.7	8.8	8.6	9.1	
Total Alkalinity	High	100	170	230	240	225	
	Low	75	106	110	142	20	148
	Mean	88	139	188	204	76	
Total Hardness	High	160	220	240	250	454	
	Low	85	130	150	163	195	211
	Mean	131	191	208	212	289	
Total Nitrogen	High	1.21	0.41	4.41	0.78	4.05	
	Low	0.24	0.22	0.04	0.37	0.84	0.86
	Mean	0.59	0.33	0.71	0.59	2.18	
Total Phosphate	High	0.34	0.14	0.16	0.38	0.53	
	Low	0.14	0.05	0.02	0.05	0.32	0.18
	Mean	0.19	0.13	0.09	0.17	0.43	

* All values in ppm

Figure 3. Total alkalinity, total hardness, pH and oxygen concentrations in the temporary pond from March 4, 1970, to July 24, 1970.

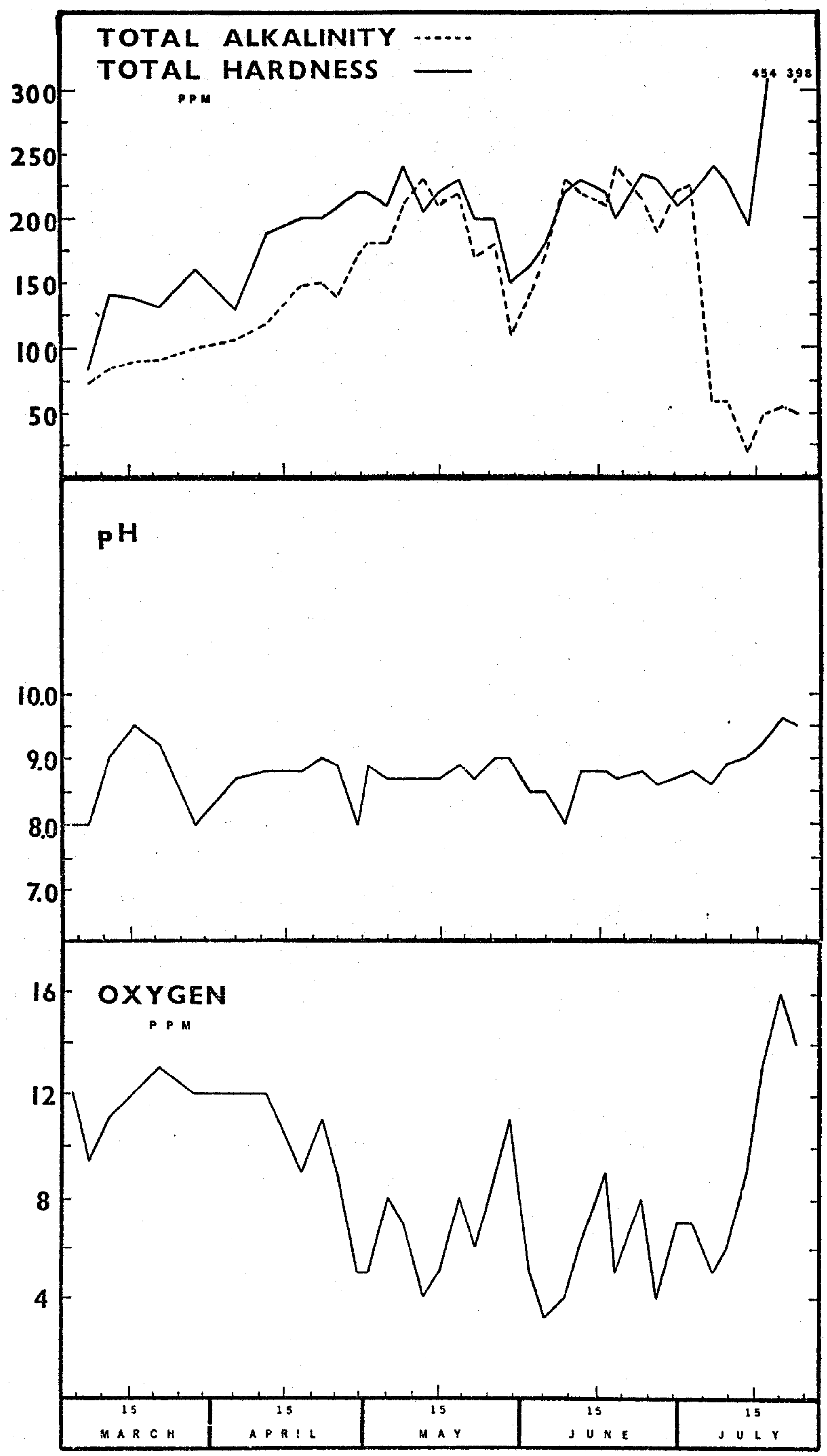
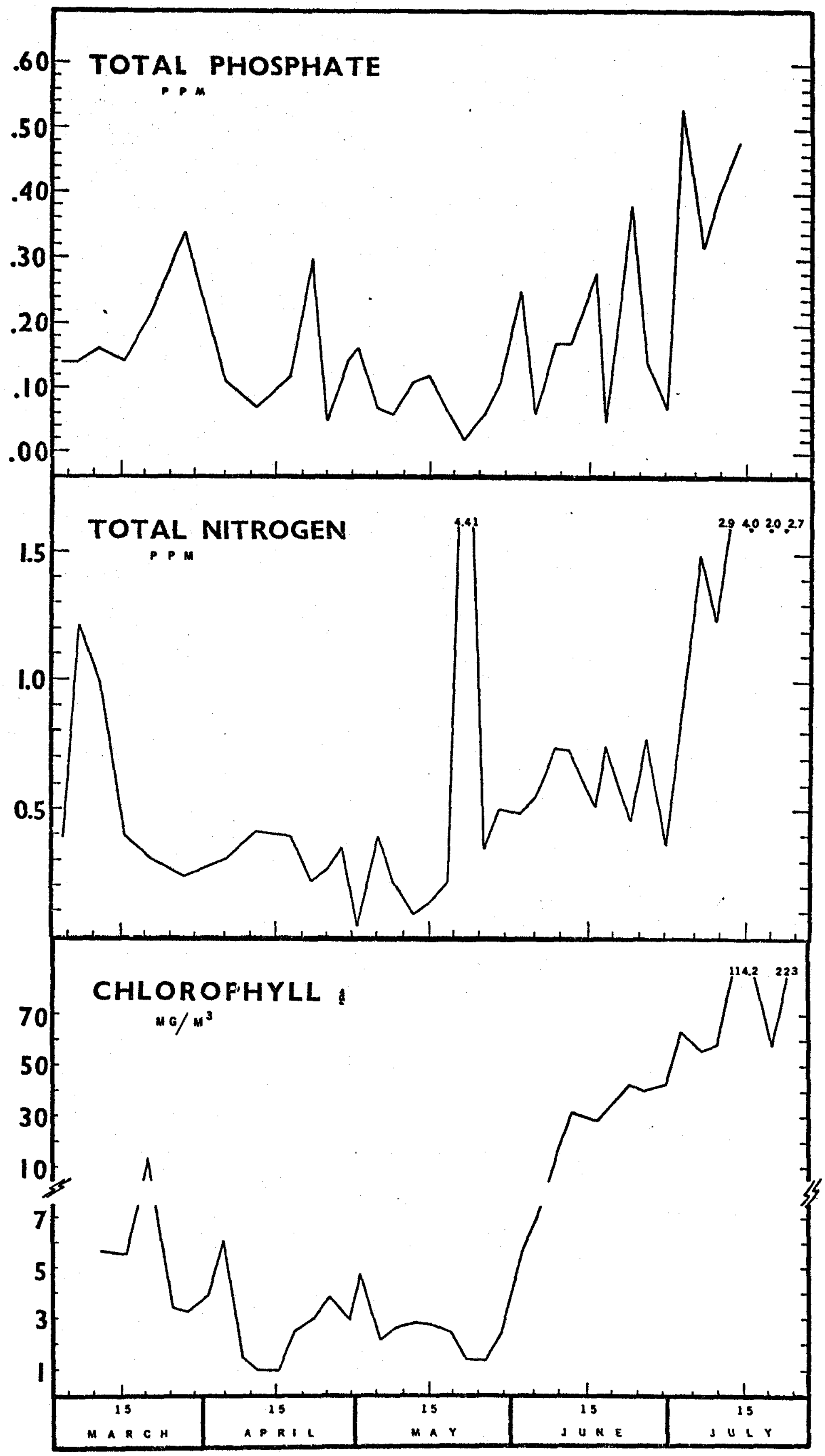

TOTAL ALKALINITY
TOTAL HARDNESS
PPM
454 398
300
250
200
150
100
50
pH
10.0
9.0
8.0
7.0
OXYGEN
PPM
16
12
8
4
15
MARCH
APRIL
MAY
JUNE
JULY

Figure 4. Total phosphate, total nitrogen and chlorophyll *a* in the temporary pond from March 4, 1970, to July 24, 1970.



TOTAL PHOSPHATE
PPM
.60
.50
.40
.30
.20
.10
.00
TOTAL NITROGEN
PPM
4.41
2.9 4.0 2.0 2.7
1.5
1.0
0.5
CHLOROPHYLL
MG/M³
114.2
223
70
50
30
10
7
5
3
1
15
MARCH
15
APRIL
15
MAY
15
JUNE
15
JULY

the mean value for North American surface waters of 0.07 ppm (Altman and Ditmer, 1966). The general trend was that phosphate increased when nitrogen decreased, and visa versa. However, like nitrogen, phosphate concentrations were highest just prior to the pond drying up.

C. Biological Results

Zooplankton

Studies have shown that Zooplankton that inhabit temporary ponds usually exhibit a limited community composition. This was likewise true of the zooplankton populations studied in this dissertation.

Of several species of Cladocera which inhabited the pond, two were Daphnia pulex and D. schødleri (Fig.5). Males of both species were present during all but the very early parts of the population cycles. However, their numbers were very low and they were not counted. Another abundant cladoceran was Moina rectirostris (Fig.5). On two separate occasions a single individual of Bosima sp. was observed.

The periodicity of the Daphnia populations were not largely effected by the changing pond volumes (Table IV). The number of times that the population increased (or decreased) over the previous sample were similar, whether considering the number per liter or the total estimated number in the pond. The only differences of any significance were at the peak population numbers (May 19 and May 22). In this case, the decrease in pond volume suggested a larger population increase than actually occured. However, it should be

Figure 5. Cladocera, total Calanoida and chlorophyll a in the temporary pond from March 4, 1970, to July 24, 1970.

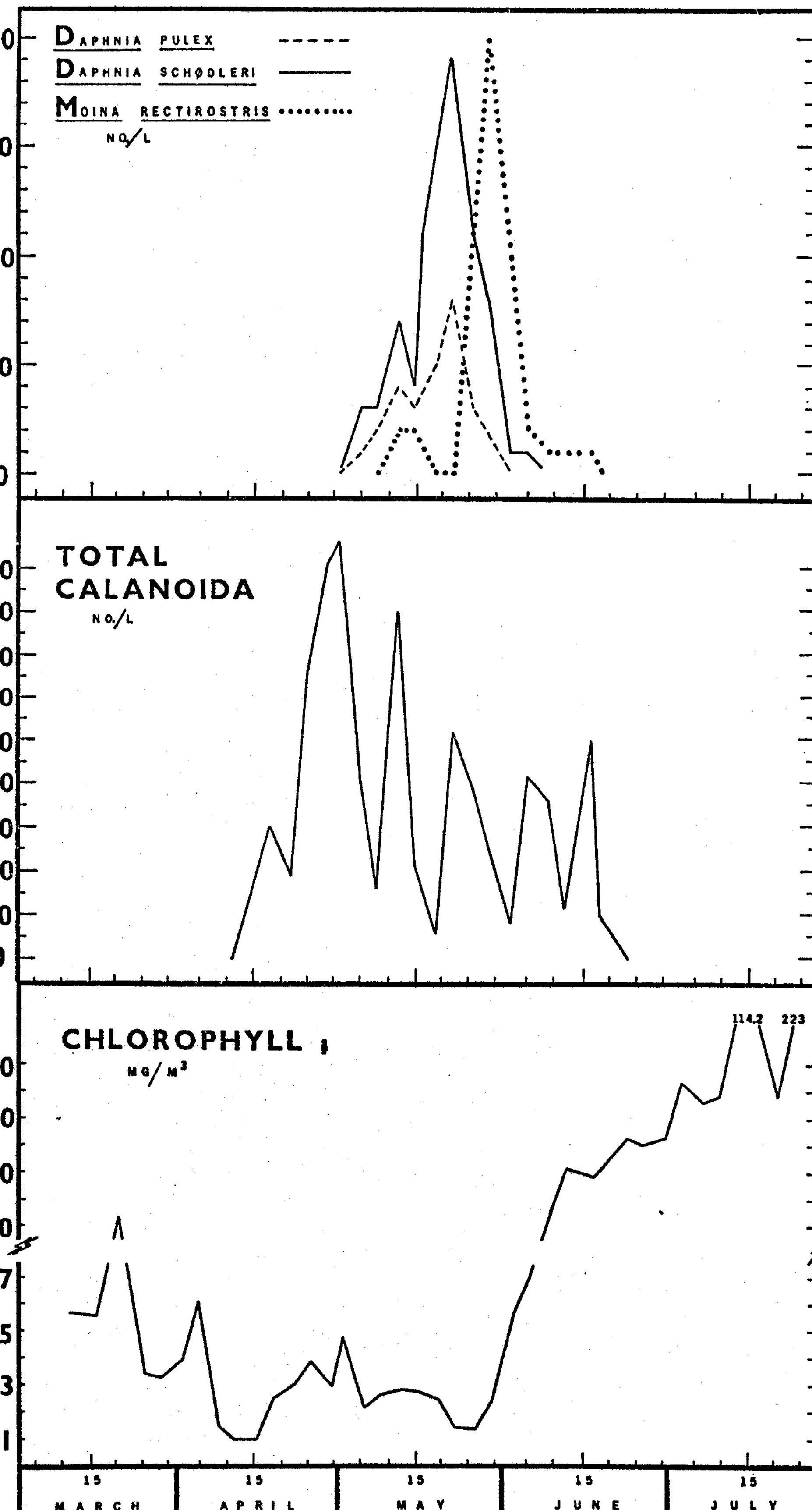

DAPHNIA PULEX
DAPHNIA SCHØDLERI
MOINA RECTIROSTRIS
NO./L
40
30
20
10
0
TOTAL CALANOIDA
NO./L
90
80
70
60
50
40
30
20
10
0
CHLOROPHYLL a
MG/M³
114.2
223
70
50
30
10
7
5
3
1
15
MARCH
15
APRIL
15
MAY
15
JUNE
15
JULY

TABLE IV. THE EFFECT OF VOLUME ON THE POPULATION NUMBER OF <u>DAPHNIA PULEX</u> AND <u>DAPHNIA SCHØDLERI</u>

Date	Total Pond Volume (Liters)	Daphnia No/L.	Schødleri X*	Total in Pond	X*	Daphnia No/L.	Pulex X*	Total in Pond	X*
1/5	206×10^3	0	-	0	-	0	-	0	-
5/5	206	6	-	1236×10^3	-	2	-	412×10^3	-
8/5	205	6	1	1230	1	4	2.00	820	1.68
12/5	204	14	2.33	2856	2.32	8	2.00	1632	1.99
15/5	204	8	0.51	1632	0.57	6	0.75	1224	0.75
19/5	169	22	2.75	3718	2.28	10	1.67	1690	1.38
22/5	146	38	1.73	5548	1.49	16	1.60	2336	1.38
26/5	140	22	0.58	3080	0.55	6	0.37	840	0.36
29/5	136	16	0.73	2176	0.71	0	0	0	0
2/6	131	2	0.12	262	0.12	0	0	0	0
5/6	122	2	1.00	144	0.55	0	0	0	0

X* The number of times the Daphnia have increased or decreased over the previous example noted that the decrease in pond volume increases the relative density of individuals.

Besides the Cladocera, the most abundant zooplankters were the calanoid Copepod Diaptomus leptopus (Fig.5), and the Cyclopoid Cyclops biscuspidatus thomasi. The rotifer species present were less abundant than in previous studies in this area (Hodgkinson,1970; Oud,1970) and were not enumerated. Since the primary interests in this study were the two species of Daphnia, the other zooplankton will not be included in the following discussion.

Daphnia Field Data

It should be noted that since the pond was very small, a sample of limited volume was necessary to avoid effecting the entire population of Daphnia. Therefore, some of the measurement data is based on a small sample size.

1. Length

Data for body measurements are shown in Table V. The range in length for the mature female D. pulex in the temporary pond was 1.22 mm to 2.00 mm from a sample size of 172 individuals. The 172 measurements were normally distributed with a mean length of 1.62 mm and a standard deviation of $\pm$0.14 mm. Of the adult D. pulex counted, 18.6% were smaller than 1.50 mm. Females that produced ephippial eggs were generally slightly larger than those that produced parthenogenetic eggs.

The range in length for mature female D. schødleri in the temporary pond was 1.20 mm to 1.90 mm. The mean length

TABLE V. SUMMARY OF DAPHNID LENGTHS

Type	Daphnia Pulex N	Daphnia Pulex $\bar{X}$	Daphnia Pulex S.D.	Daphnia Schødleri N	Daphnia Schødleri $\bar{X}$	Daphnia Schødleri S.D.
Parthenogenetic Females	38	1.57	$\pm$ 0.12	99	1.44	$\pm$ 0.12
Ephippial Females	134	1.63	$\pm$ 0.14	109	1.55	$\pm$ 0.10
Total Female Population	172	1.62	$\pm$ 0.14	208	1.50	$\pm$ 0.12

was 1.50 mm with a standard deviation of ± 0.12 mm for the 208 individuals measured. Like D. pulex, females that produced ephippial eggs were generally larger than females that produced parthenogenetic eggs.

2. Brood Size

The average brood size determined for both species of Daphnia are summarized in Table VI. Only those daphnids that retained their brood eggs in formalin preservation could be counted. From a total of 38 adult parthenogenetic females the mean brood size for D. pulex was 3.95 eggs, with a standard deviation of ± 1.80 eggs. Daphnia schødleri had a mean brood size of 3.48 ± 1.35 eggs, from a sample size of 99 individuals.

Since there are two ephippial eggs per female in both species of Daphnia, it is sufficient to count the number of females of each species bearing ephippia to determine total ephippiation.

3. Ephippial Production

To distinguish the immature eggless instars from the mature "eggless" instars in D. schødleri, those that had a length greater than 1.26 mm were considered as adult. Similarly, D. pulex greater than 1.30 mm in length were considered as mature.

In D. pulex, the mean length of 51 mature females was 1.62 ± 0.16 mm. A t-test showed no significant difference between these females and those that had retained their eggs. Using normal probability paper (Southwood, 1966) the entire

TABLE VI. BROOD SIZE AND BODY LENGTH

Date	DAPHNIA PULEX No. of Ind.	DAPHNIA PULEX $\bar{X}$ No. of Eggs	DAPHNIA PULEX Mean Size	DAPHNIA SCHØDLERI No. of Ind.	DAPHNIA SCHØDLERI $\bar{X}$ No. of Eggs	DAPHNIA SCHØDLERI Mean Size
5/5	1	1	1.22	8	4.50±1.32	1.34±0.09
12/5	7	4.00±1.60	1.52±0.13	3	3.00±1.41	1.55±0.08
15/5	0	0	0	3	3.33±1.88	1.49±0.08
19/5	4	4.00±2.20	1.70±0.13	10	3.60±0.92	1.46±0.07
22/5	15	3.27±1.30	1.54±0.09	17	3.47±1.09	1.50±0.08
26/5	10	4.20±0.75	1.58±0.07	22	3.54±1.40	1.67±0.11
29/5	1	5	1.54	16	2.69±1.16	1.51±0.08
2/6	0	0	0	20	3.70±1.34	1.31±0.06
5/6	0	0	0	0	0	0
Total Pop'n	38	3.95±1.80	1.57±1.20	99	3.48±1.35	1.44±0.12

sample counted ("eggless adults plus those with eggs) showed a normal distribution for lengths. Therefore, statistically the"eggless" D. pulex greater than 1.30 mm were the same population as the D. pulex with eggs.

In D. schødleri, the mean length for 89 females was 1.40 ± 0.09 mm. This is significantly different from the egg bearing adults. However, these "eggless" adults were not normally distributed (using probability paper) so the test for significant difference cannot be used in this case. The majority of these females were from 1.30 mm to 1.54 mm in length. Despite the fact that a simple statistical method could not be applied, D. schødleri greater than 1.26 mm in length were accepted as adults. This is not an unreasonable biological assumption since the normal range for adults reported by Brooks (1957) is 1.20 mm to 2.00 mm. Also, the range in length for adult females in the temporary pond was 1.20 mm to 1.90 mm.

After the total number of adults was determined, the extent of ephippial production for the two species of Daphnia was calculated (Fig. 6 and 7 and Tables 7 and 8). The index of ephippial production was the ratio of the ephippial females (e) to the parthenogenetic females (p). If the e/p ratio is greater than unity, this indicates that there is a greater production of ephippial females over parthenogenetic females. Comparing the two Daphnia populations, of the total adult D. pulex sampled, 60 per cent produced ephippial eggs as compared to 36 per cent for D. schødleri.

TABLE VII. EPHIPPIAL PRODUCTION OF DAPHNIA PULEX

Date	Parthen. Females with Eggs (1)	Eggless Parthen. Females (2)	(1)+(2)=p	Ephippial Females	e/p
5/5	1	1	2	0	All p
8/5	0	2	2	0	All p
12/5	7	1	8	15	1.88
15/5	0	4	4	0	All p
19/5	4	8	12	9	0.75
22/5	15	26	41	70	1.71
26/5	10	5	15	23	1.53
29/5	1	4	5	14	2.80
2/6	0	0	0	1	All e

TABLE VIII. EPHIPPIAL PRODUCTION OF DAPHNIA SCHØDLERI

Date	Parthen. Females with Eggs (1)	Eggless Parthen. Females (2)	(1)+(2)=p	Ephippial Females (e)	e/p
5/5	8	3	11	0	All p
8/5	0	0	0	0	-
12/5	3	7	10	4	0.40
15/5	3	5	8	1	0.13
19/5	10	32	42	6	0.14
22/5	17	21	38	16	0.42
26/5	22	5	27	19	0.70
29/5	16	9	25	51	2.04
2/6	20	6	26	7	0.27
5/6	0	1	1	0	All p

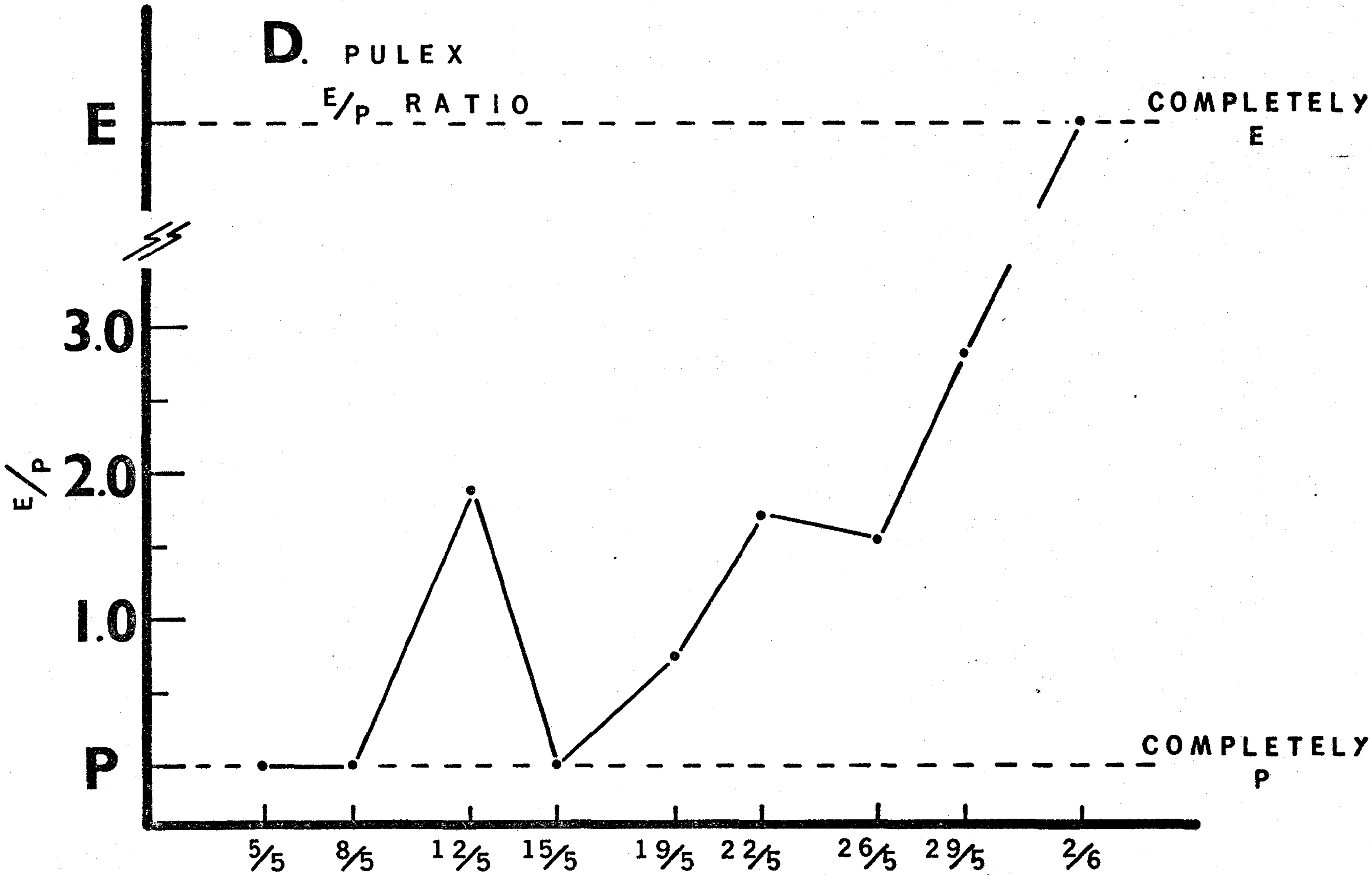


Figure 6. The ratio of the ephippial females (e) to the parthenogenetic females (p) for Daphnia pulex in the temporary pond.

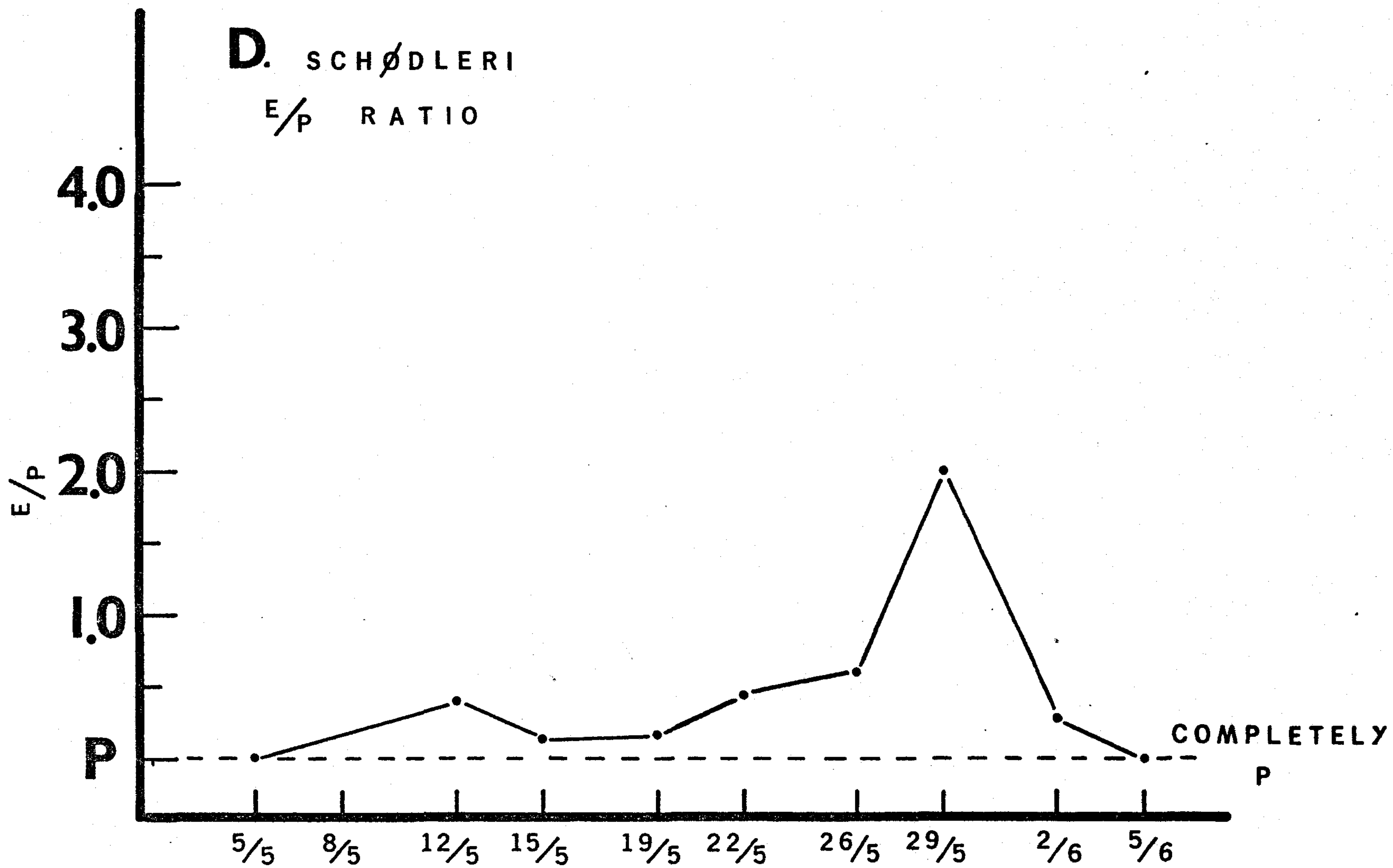


Figure 7. The ratio of the ephippial females (e) to the parthenogenetic females (p) for Daphnia schødleri in the temporary pond.

Phytoplankton

Phytoplankton standing crops as available food for the Cladocera, was determined as chlorophyll a concentrations and is shown in figure 5.

No direct correlation was found between total zooplankton and chlorophyll a concentrations in agreement with the findings of O'Brien (1971).

DISCUSSION

Daphnia are particularly suitable material for ecological study. The genus exhibits a world wide distribution with 30 of a probable 50 species characterized (Brooks, 1957). They are common zooplankton of most freshwater lakes and ponds, and can usually be found in the quiet sections of rivers and streams. Most of these populations usually exist year around, although their numbers may fluctuate. Post-egg populations of the two species in this pond flourished over approximately a one month period despite the presence of water over longer periods of time.

In this study, two questions were asked. First, does the temporary pond through natural selection exhibit an effect on the life cycle of *Daphnia*? Second, upon what life history functions does the pond act to enable the *Daphnia* to maintain their existence?

In response to these questions, the *Daphnia* were examined for age of reproductive maturity, brood size, and ephippial production.

Age Of Reproductive Maturity

In *Daphnia* there is no metamorphosis during its growth and maturation. The young *Daphnia* are liberated from the mother's brood pouch as miniature immature adults. Growth occurs immediately after molting while the integument is still soft. Once the integument has hardened, there is no increase in size until the next molt. After molting, the increase in size is rapid. For *Daphnia magna* this is completed in less than a minute (Edlen, 1937). *Daphnia* growth rates are rapid at first, then decrease to a very low level in later instars. MacArthur and Baillie (1929) found that the growth curve of *D. magna* became asymptotic at a length of about 2.7 mm. Sometimes there is a slight decrease in length in the latest instars, as Banta (1939) found in *D. longispina*.

Life stages in *Daphnia* consist of egg, pre-adult or immature instars, and adult or mature instars. The number of immature instars is fairly small and range from four to six. Adult instars are of a greater magnitude, with as high as twenty-four in *D. magna* (Edlen, 1943). Anderson *et al* (1937) found a total of twenty stages in *D. pulex*, four of which are immature and sixteen mature. No data is currently available for *D. schødleri*.

The age at which individuals reach reproductive maturity will have a significant effect on population growth. Eggs produced at an earlier age will have a greater effect on the intrinsic rate of increase than those produced at a later age. Anderson *et al* (1937) have determined the mean length for each instar of *D. pulex* from laboratory cultures (Appendix I, Table I). The immature instars (1 to 4) range from 0.567 mm to 1.265 mm, while maturity is reached at about 1.608 mm. The difference between maturity and immaturity is about 0.34 mm.

The body length for North American *D. pulex* is reported by Brooks (1957) as being between 1.5 mm amd 2.5 mm. The range in length for mature *D. pulex* in the temporary pond was 1.22 mm to 2.00 mm. These adults were therefore smaller than normally reported. On the basis of Anderson's 1937 data (Appendix I, Table I) and that of Green (1956), two possibilities may exist for the establishment of the reproductive pattern: 1) the Daphnia population becomes reproductively mature by the fourth instar; one instar earlier than reported, 2) the Daphnia population completed five instars but since its mean length per instar was less than normal, its body length at maturity was smaller than reported in the literature. If the first theory is correct, then it is possible that conditions in the temporary pond have modified the life cycle of D. pulex.

It appears that there is selection for those individuals that reach an early reproductive maturity. Eggs produced at an early age have a greater effect on the intrinsic rate of increase of the population, a selective advantage that allows the population to establish itself in the short period of time that water is present in the pond. It is also advantageous for population growth to produce earlier clutchs, even if smaller in number, than a larger clutch at a later period.

It is of interest to consider the maximum length of D. pulex from the temporary pond. Since the length did not exceed 2.00 mm, it would appear that these Daphnia did not live past the eighth instar. This suggests that there is no selection for longevity. Since each instar is capable of producing a clutch of eggs, it seems that a long term population contribution is not advantageous. On the contrary, the earliest is important. The trend in this case is, therefore, one of establishing, rather than one of maintaining the population.

Although there is no data on instar length for D. schødleri, the evidence does not indicate selection for earlier maturation. This is suggested by the fact that the size range for adult D. schødleri in the temporary pond was similar to that reported by Brooks (1957). Also, it is thought that the selective pressures for early maturation were probably not as great since it is a small daphnid comparable in size to D. ambigua, a species that matures by the fourth instar (Green. 1956).

Clutch Size

Fecundity is another important parameter when considering population growth. At the beginning of the study, it was suspected that the clutch size of the daphnids would be larger. I thought that the temporary pond would select for those individuals that produced the largest number of eggs. This was not the case.

Green (1956) reporting on the clutch sizes of D. pulex from three Danish localities found a range of 4 to 16 eggs per clutch. The largest clutch size for D. pulex from the temporary pond was only 7 eggs with an average for the population of 3.95 eggs.

Wright (1965) recorded the clutch sizes for D. schødleri in Canyon Ferry Reservoir, Montana, of 2 to 13 eggs, with the average clutch size for the entire sample of 5. Daphnia schødleri in the temporary pond had an average clutch size of 3.48 eggs, with the largest clutch having 7 eggs. Neither D. pulex nor D. schødleri in this pond study produced clutchs as large as those reported in the literature.

Several environmental factors could account for the lower fecundity levels found in the temporary pond. Tauson (1930) found that temperatures of 15°C to 25°C were favorable for egg production in D. pulex. Temperatures above and below this range caused a considerable decrease in the number of eggs produced. But temperatures in the temporory pond during the time when Daphnia were present, only exceeded 25°C once (May 25 when the temperature was 26°C), and never fell below 15°C. However, since the temperatures were taken at 10:30 am, the pond may have been slightly cooler than it would have been during the hottest part of the afternoon.

Oxygen concentrations are also important to egg production. Fox et al (1951) reported that a lack of oxygen retards egg production in D. magna. Green (1956) confirmed this effect on D. obtusa. If the oxygen concentration of the water falls below 2 to 3 ppm, the number of eggs produced also decreases. On only two occasions, while Daphnia were present in the pond, did the oxygen concentration drop to 4 ppm or lower. Therefore, the effect of oxygen concentration as limiting to egg production is probably minimal.

Although no direct correlation between alkalinity, hardness, and phosphate and the Daphnia population growth rate was found, the possibility exists that with the increase in salt concentration due to evaporation, reproduction and embryonic developement may have been effected. Hazelwood and Parker (1963) have found a negative correlation with increasing salt concentration in a population of D. schødleri in Kepple Lake, Washington.

Probably the greatest limiting factor to clutch size for the Daphnia in the temporary pond is body size. Green (1956) found that the general tendancy was for egg number to increase with increasing size. Therefore, the smaller size of the Daphnia in the temporary pond would tend to restrict the clutch size.

Ephippial Production

In a temporary pond ephippial production is essential. If ephippia are not produced the Daphnia will become extinct. Once the pond dries out, the daphnids that have not produced ephippia during their life cycle cannot contribute to the next population. Therefore, selection will be for those that do produce ephippia.

At the beginning of this study, I felt that the temporary nature of the pond would have a direct influence upon the extent of ephippiation. Ephippial production should be enhanced since these daphnids that did not produce ephippia would be eliminated from the following population. I also thought that ephippial production would take place early in the life cycle, a result of the varying lengths of time the pond contained water. A dry warm spring and early summer would dry the pond out early thereby selecting those daphnids that produced ephippia early in their life cycle.

To my knowledge, no data on the extent and periodicity of ephippial production has been recorded in the literature for natural populations of D. pulex and D. schødleri. Therefore, a comparison of ephippial production in the pond with other natural systems is not possible here. This discussion is limited to a comparison of the two daphnid populations, and the possible influence of the temporary pond.

The manner in which both populations of Daphnia produced ephippia differed. D. pulex produced ephippia at a much greater rate than D. schødleri. In Daphnia pulex, all of the reproductive females early in the life cycle were parthenogenetic. The only exception to this was on May 12 when the ephippial females outnumbered the parthenogenetic females. This period of parthenogenetic reproduction was followed by a high rate of ephippial reproduction. Since most of the eggs were ephippial, there were very few young recruits into the population with the result that D. pulex was eliminated for that season.

Ephippial production of D. schødleri was not as great as D. pulex. Although ephippia were present during most of the life cycle in substantial numbers (10 to 40 per cent), parthenogenetic females were more abundant (Fig. 7). The only time that ephippial females outnumbered parthenogenetic females (approximately twice as many) was just prior to the end of their life cycle.

The extent that the temporary pond has influenced the daphnid ephippial production is difficult to determine. The ephippial production of D. pulex was generally, as expected, a high rate of ephippial production throughout most of the life cycle. This did not occur for D. schødleri. In both cases, however, the longevity of the two Daphnia species was limited to approximately one month. In that time a sufficient number of ephippia were produced to allow the population to overwinter while the pond was frozen or dry.

Another factor that may influence ephippial production is interspecific competition. Frank (1957), raising D. pulicaria and D. magna in the laboratory found that D. pulicaria always displaced the larger D. magna. Daphnia magna did not become extinct but was inactivated through the production of ephippia. In the temporary pond, D. schødleri is smaller than D. pulex and apparently more successful due to its greater numbers. This would indicate that besides the selective pressures on ephippial production by the nature of the temporary pond, there is also competative pressures inducing D. pulex to produce ephippia. The final result would be a much greater rate of ephippial production by D. pulex. This would explain why the rate of ephippial production of the two species of Daphnia differed. The effect of interspecific competition on the Daphnia by the Copepoda is probably negligeable (Parker, 1960; 1961).

CONCLUSIONS

The life cycles of Daphnia pulex and D. schødleri were modified by the temporary nature of the pond. This was most apparent in D. pulex where the adult females were smaller in the temporary pond than is usually found in permanent aquatic habitats. This, together with a high rate of ephippial production are probably the two most important factors that have been modified to ensure that the population will survive and establish itself.

In Daphnia schødleri ephippial production was lower than D. pulex. However, because of its larger population number, ephippial production was sufficient to maintain its population from one season to the next.

The selective pressures of the temporary pond on Daphnia schødleri were apparently not as great as those on D. pulex. Daphnia pulex was less abundant than D. schødleri and therefore a much greater rate of ephippial production was essential to maintain its population from year to year.

SUMMARY

1. The object of this study was to determine if the temporary nature of the pond habitat had modified the life cycle of its *Daphnia* populations.
2. A twice weekly sampling programme to determine physical, chemical and biological characteristics of the pond was established from March 4, 1970, when the pond thawed, to July 24, 1970 when the last sample was taken before the pond had dried.
3. Nitrogen, phosphate, chlorophyll *a*, oxygen and turbidity were the highest prior to the pond dring. Total alkalinity decreased sharply at this time.
4. The most abundant zooplankton were three cladoceran species: *Daphnia pulex*, *D. schødleri* and *Moina rectirostris*; and two copepod species: *Diaptomus leptopus* and *Cyclops bicuspidatus thomasi*.
5. The *Daphnia* population numbers were not largely effected by the changing pond volumes except at peak population numbers. The decrease in pond volume at this time suggested a larger population increase than actually occured.
6. The body length at which *D. pulex* became reproductively mature was less in the temporary pond suggesting fewer molts and therefore a younger *Daphnia*. *Daphnia pulex* probably became reproductively mature by the fourth instar. The body length at which *D. schødleri* became reproductively mature was consistent with those reported in the literature.

7. The species of *Daphnia* investigated exhibited clutch sizes comparable to that reported in the literature. Body length probably limited clutch size.
8. A high rate of ephippial production was characteristic of *D. pulex* during most of the life cycle. In *D. schødleri* parthenogenetic females were most abundant, but ephippia were produced in substantial numbers during most of the life cycle.
9. The greater rate of ephippial production by *D. pulex* was probably related to congeneric competition.
10. The influence of the temporary nature of the pond on the life cycles of the two species of *Daphnia* is more apparent in *D. pulex*.

APPENDIX I

Table I. Mean instar lengths for *D. pulex* from Anderson *et al* (1937)

INSTAR	INSTAR LENGTH (mm)
1	0.5665±0.0034
2	0.7214±0.0038
3	0.9609±0.0056
4	1.2653±0.0092
5	1.6079±0.0095
6	1.8134±0.0106
7	1.9332±0.0117
8	2.0571±0.0130
9	2.1673±0.0126
10	2.2466±0.0116
11	2.3061±0.0108
12	2.3401±0.0099
13	2.3705±0.0092
14	2.3853±0.0095
15	2.4032±0.0092
16	2.4223±0.0085
17	2.4461±0.0072
18	2.4604±0.0072
19	2.4835±0.0072
20	2.4890±0.0072

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